able on the under side of the head and on the front coxae; and in the variable but weak infuscation of the gaster.

This common ant is widespread and will very probably be found in Utah, Idaho and Mexico. It appears to be largely crepuscular or nocturnal. W. S. Creighton *in litt.* said "—as regards the Dateland, Arizona specimens I can give you a fairly reliable picture of the circumstances under which they were taken even though the field notes for the trip are at the island. In 1952 the highway that runs through Dateland was a dividing line between irrigated land to the south and non irrigated desert to the north. The irrigated area supported, as you would expect, an extensive stand of date palms. The non irrigated area consisted of a sandy area of small dunes about 10–15 ft. high. There were a few bushes and considerable bunch grass but the place was not nearly so sandy as Grey's Well, California, although the sand seemed less prone to shift. We arrived at the station just before dusk and while supper was being prepared, I found the *Aphanogaster* colony which had begun to forage in the dusk and kept it up after dark. There is no doubt that the thing is nocturnal and, what is more, it has its marriage flight at night!—The nest was not at all conspicuous since it consisted of a single nest opening with no crater or mound. I suppose that is because the excavated material is soon displaced by the wind."

R. R. Snelling, who collected the species in Malheur County, Oregon, reported *in litt.* as follows, "These were taken at approximately 10:30 P.M. while foraging. The night was quite cool, 50–52 Fahr., and windy. The sky cloudy, with occasional light showers at the time of the collection. The ants were quite active, and very difficult to capture because of their color and rapid movement. If the color, which blended quite well with the soil, is any indication at all, this species may well be a regular night forager. That the ants were active at such relatively low temperatures would seem to support this view."

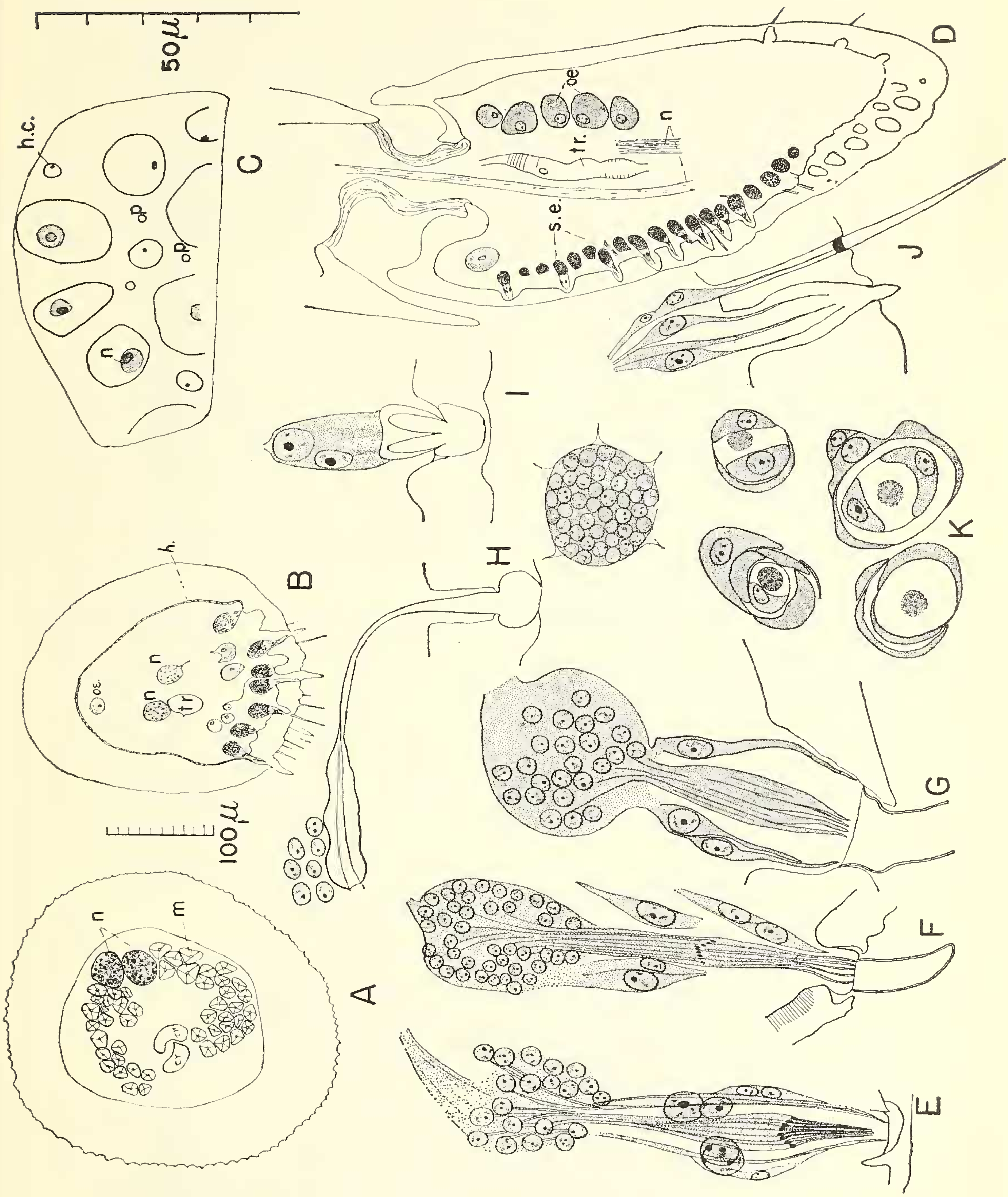
THE ANATOMY OF THE ADULT QUEEN AND WORKERS OF THE ARMY ANTS *ECITON BURCHELLI* WESTWOOD AND *ECITON HAMATUM* FABRICUS

ROY M. WHELDEN

[CONTINUED]

THE ANTENNAE

Early in this paper, the presence of a thickened area in the hypodermis in the antennae was noted (Fig. 16, B). In the head, at the base of each antenna, is a small gland composed of about a dozen cells in the queens and of three or four in the workers. The ducts of these cells open through the mem-


A
B
C
D
E
F
G
H
I
J
K
50μ
100μ
h.c.
n
m
oe.
tr.
s.e.
h.

brane which joins the antennal wall to that of the head. In minor workers this gland may be reduced to a single cell, easily missed if the section is not cut at exactly the right place to show its presence.

The scape offers little of particular interest, its most conspicuous contents being the two relatively large muscles and nerves; in addition to these, are small tracheal branches and an occasional fat cell. The walls of the scape are thick, commonly measuring 50–60 μ and less often reaching 70–80 μ.

The funiculus is more interesting than is the scape. Hairs are relatively few on the scape and usually small, with only a few conspicuously long slender ones, mostly near its apex; whereas all segments of the funiculus are uniformly clothed with hairs. These vary some being slender, acute and 40–50 μ long, others stouter and equally acute, but 70–80 μ long: only near the apex of each of ten lower segments, and uniformly over the entire surface of the eleventh segment, do conspicuously longer and stouter hairs 150–220 μ in length occur. These are tactile hairs similar to those on the body.

In contrast the specialized sensory elements so characteristic

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FIG. 13. Antenna.

- A t.s. upper part scape of *E. hamatum* worker, nerves (n.), trachea (tr.) and muscles (m.)
- B t.s. flagellum, showing unilateral sensory elements, two nerves (n.), trachea (tr.), oenocytes (oe.) and thin hypodermis (h.)
- C tg.s. ventral wall, pores (p.), hair canals (h.c.) and nerves (n.)
- D l.s. apical segment of queen flagellum, nerves (n.), trachea (tr.), oenocytes (oe.) and sensory elements (s.e.)
- E Nerve elements in nearly mature medium worker pupa
- F Corresponding elements in callow adult worker
- G Basiconic sensilla, similar to E and F, from near base of a middle segment of mature major worker flagellum
- H Sensilla ampullaceum or flask-shaped organ of Forel
- I Champagne-cork organ of Forel partially sunk in body of sensory region
- J Antenna callow worker, tactile hair and its nerve (right) and sensory organ with nerves (left)
- K t.s. series through sensory element resembling G. Above, region of small nuclei, two sections in basal half of region of large nuclei. Below, two sections, (right) above middle and (left) near apex of sensory element

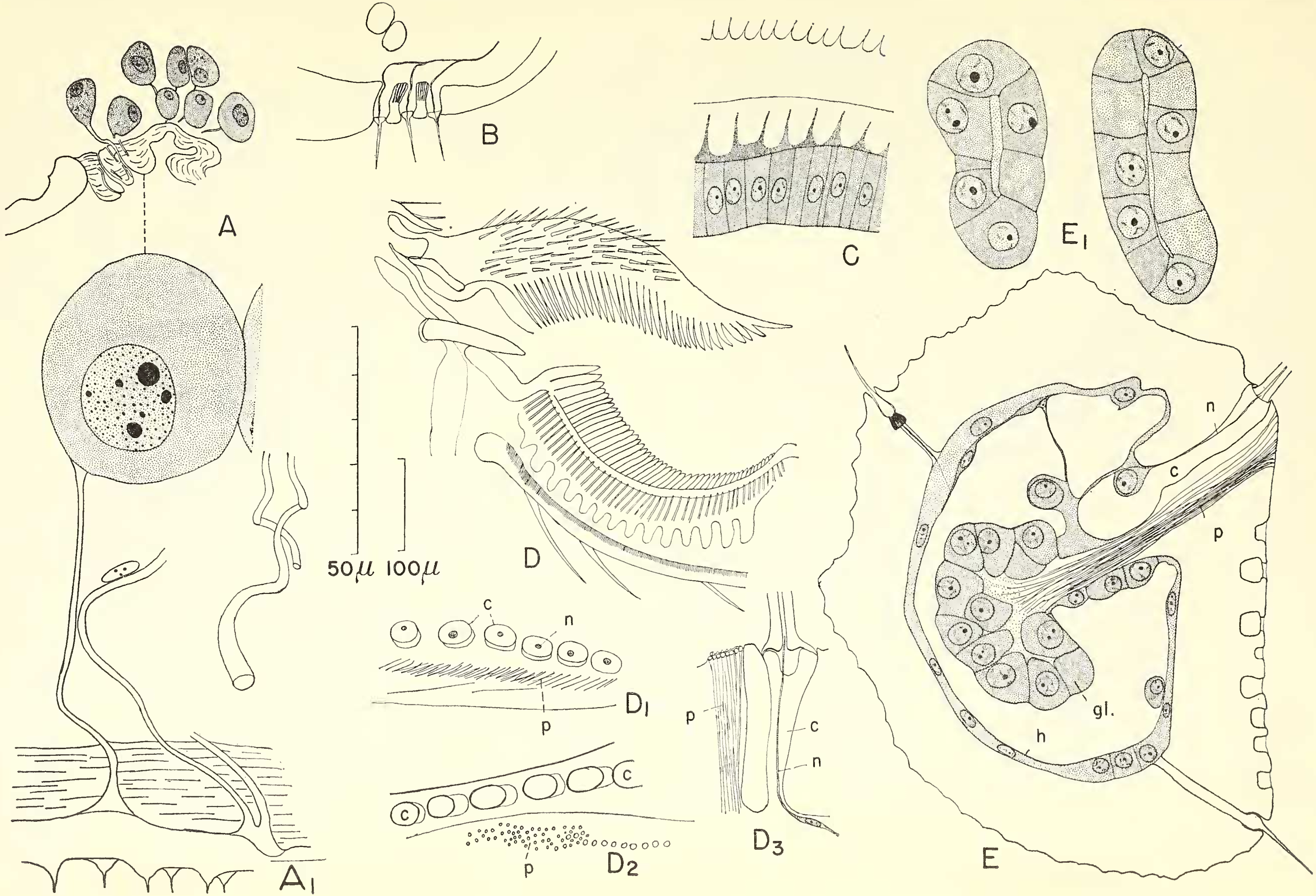
of ant antennae are limited to less than one quarter of the circumference of the funiculus (Fig. 13, B). In nearly all the individuals studied, this sensory sector forms a spiral band from the basal to the apical segments. The occasional examples in which this band was nearly straight suggest the possibility that a sweeping movement of the funiculus also causes a slight revolving of each segment over the one below it, the sum of these rotary movements resulting in the spiral appearance. Since no muscle tissue is found in the funiculus, such movement is strictly mechanical, possibly due to the asymmetrical shape of the wall at the base and the apex of each segment. The membrane connecting any two segments is also asymmetrical, being wider and much thicker on one side than on the other.

This asymmetry is more obvious internally, especially in callow insects. Callow queens have numerous oenocytes which form a uniform layer under the wall of the segment, a layer broken only by the sensory sector. Even here, oenocytes may be found beneath the cellular element associated with the sensory structures. Within the layer of oenocytes, two large nerves, and tracheal branches are found, extending nearly to the apex of the ultimate segment. Numerous fine nerves pass from the main nerves to peripheral tactile and sensory hairs; small tracheal branches are also present.

The sensory elements are similar to those found in other ants. The basiconic sensilla, having a stout strongly curved spine with bluntly rounded apex is an obvious feature (Fig. 13, E, F, G). They first appear late in pupal development; at which time, the cellular elements characterizing them are well developed, and including the group of small nuclei from the center of which a bundle of nerve fibres extends outwards. Surrounding this is a group of nuclei, several of them many times larger than the small nuclei of the lower group, and several small ellipsoid nuclei, all in coarse cytoplasmic strands extending to the surface of the developing antenna. Within these, the compact group of nerve fibres continues and is made conspicuous by the presence of a cone-shaped group of deeply staining ellipsoid bodies, one in each nerve fibre (Fig. 13, E, F). Above these bodies, the nerve fibres form a rapidly narrowing bundle ending beneath the inner surface of the wall (Fig. 13, E). In older pupae and in newly emerged callows, the structure remains much the same; but the large group of basal nuclei is now surrounded by a limited mass of cytoplasm, the group of deeply staining bodies is less conspicuous, the bodies distinctly smaller, the wall of the antenna is now well-formed and the external spine well-developed but still small (Fig. 13, F). In older ants, all trace of the small darkly stained bodies is gone (Fig. 13, G). Fig. 13, K shows a series of cross-sections through one of these basiconic sensillae, the upper one showing the compact mass of small nuclei, the lower four, different levels through and above the group of large nucleate elements.

Less conspicuous and not numerous are the small peg-like elements shown at the left in Fig. 13, J with its group of slender nerve ends extending into the cavity in the wall: the element at the right in the same Fig. 13, J is one of the small tactile hairs occurring among the sensory elements as well as over the remaining surface of the funicular segments.

Separation of the ampullaceous sensillae (Fig. 13, I) and the flask-shaped organs of Lubbock and Forel (Fig. 13, H) is difficult in these two species of *Eciton.* Between a typical ampullaceous sensilla and a typical flask-shaped organ, the intermediate elements are so finely graded that no real separation into groups is possible. Equally difficult is it to find a flask-shaped organ to describe as typical: the thick basal portion may be very short, its length scarcely exceeding its diameter; or the length may be five times the diameter; the basal end may be broadly rounded, or nearly flat; if flat, it may be at right angles to the long axis, or it may form an angle of 40° with that axis; its lateral walls may be straight, or thrown into regular undulations, or the undulations may be uneven; the central lumen may be of uniform diameter throughout, or it may narrow gradually from base to apex; and may even seem to extend below the base as in Fig. 13, H; the slender tube connecting the apex of the basal portion to the wall of the antenna may be many times the length of the basal portion, or it may be very short; it may be of uniform diameter throughout, or it may flare conspicuously as it passes through the thickness of the wall; and finally, by gradual stages a typical ampullaceous sensilla, is seen all in a single antenna. This is the condition found in certain individuals; in others, there is no indication of transition from one type of element to another.


A
B
C
E1
D
50μ 100μ
c
n
p
D1
c
c
p
D2
p
c
n
D3
n
c
p
gl.
h
E
A1

LEGS

The small glands found in the ventral part of the thorax, at the base of each leg (Fig. 14, A) have already been mentioned. Similar glands are found in the distal end of each segment. The number of cells found in each gland mass varies slightly in any form, much more when various forms are compared. The gland mass found in the coxal segment, with ducts opening through the membrane joining the segment to the trochanter varies from 8–10 cells in queens; 5–7 cells in large and medium workers; and 4–5 cells in minors. In lower segments, the number of cells in any gland seem to be less than in the upper segments. Often, gland cells are absent in tarsal segments of the smaller forms, which may be factual or merely that it is difficult to recognize a gland cell because of an unsuitable—angle of sectioning: recognition is often made more difficult by the large number of oenocytes present in the segments of the legs—but oenocytes are usually recognizably larger. It is probable the gland cells are always present, but reduced to 2 or 3 cells, or to a single cell.

Fig. 14. Leg detail.

A Gland at hindleg base *E. hamatum* queen with (below) detail of cell, ducts and openings through membrane joining body to leg and bristly outer surface.

B Part of wall of basal coxa of worker front leg, minute spines and nerves passing into them

C Section of apex of tarsus above comb, thick hypodermis, thick chitin wall with darkly stained cusps in endocuticle and fine bristles from cuticle

D Strigil with pectinate spur, comb and chitin walls

D_1 Section parallel to surface of comb, large canals (c.) to bases of coarse spines of comb and central nerve fiber (n.) passing into spines, and row of fines pores (p.)

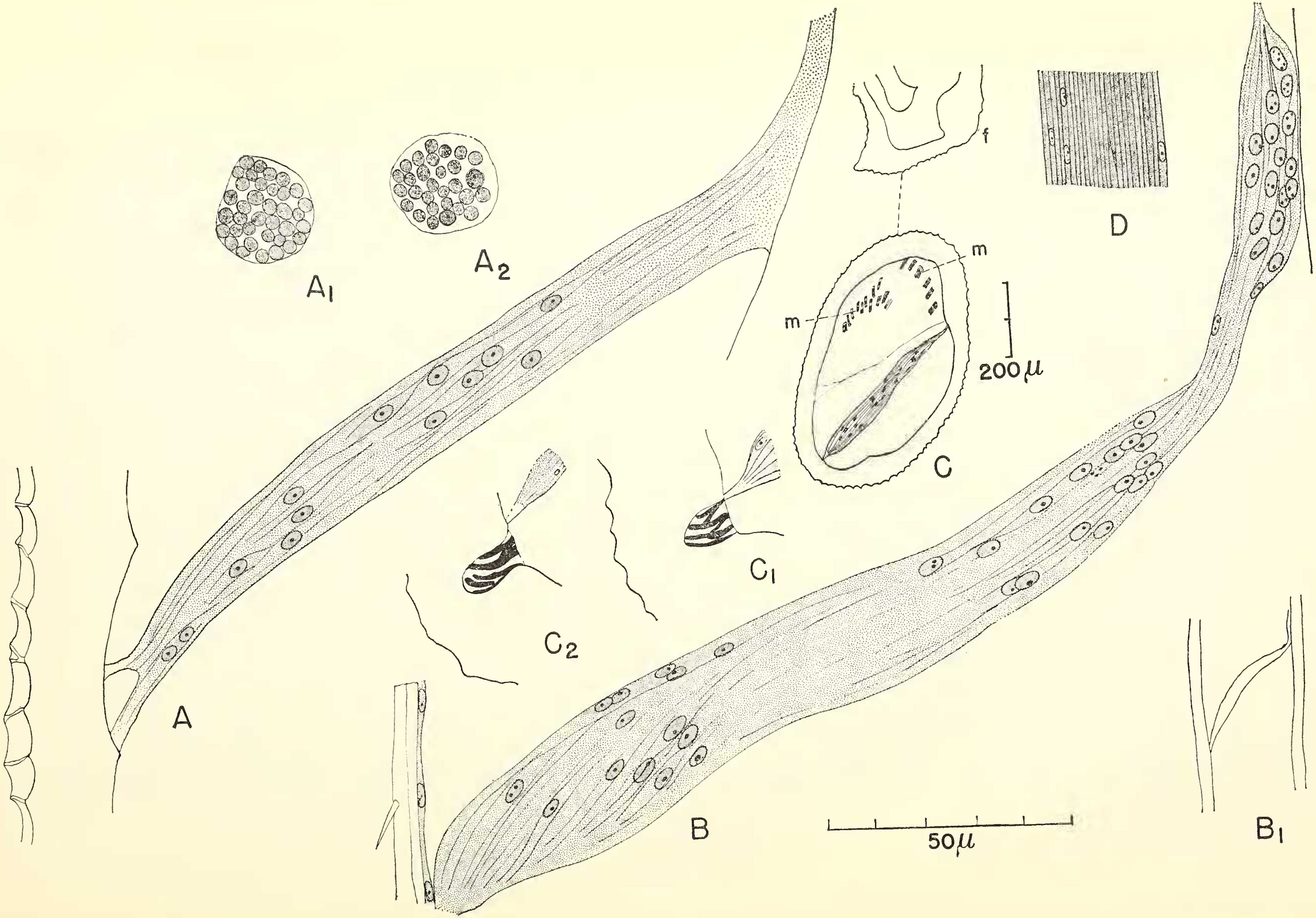
D_2 Section beneath D_1 and at right angle to tarsus face

D_3 Detail section cut at right angle to long axis of tarsus, fine nerve (n.) through coarse canal (c.) into base of spine of comb and a group of fine pores (p.) through chitin wall

E t.s. metatarsus of *E. hamatum*, outer wall, hyopdermis (h.) coarse canal (c.) and fine pores (p.) and section metatarsal gland (gl.)

E_1 t.s. two successive lobes of gland

Scale: A, B and D = 100 μ scale; others = 50 μ scale


A
A1
A2
B
B1
C
C1
C2
D
m
m
f
50μ
200μ

The sclerotic wall of the legs of *Eciton* measures 35–50 μ. The hypodermal layer just beneath the wall varies greatly, not only in different areas, but also in the same area in different individuals. In one such area, in a queen, the hypodermis was uniformly only 2 μ thick; the corresponding area, in another queen, was 11–12 μ thick. Conspicuous in both workers and queens, was a thick hypodermal layer over the upper part of the thick membranes connecting the walls of the segments. Often these cells were 30 μ thick, and resembled a large gland.

The structure of the wall at some of the joints folds back extensively, forming narrow rings 200 μ or more in length, which in some cases overlap the wall of the succeeding segment, and in others extend under the wall of the preceding segment. In one case, where the femur joined the tibia, the external surface of the outer wall of the upper end of the tibia projected into a mass of slender spines 20–25 μ long. This area is nearly 250 μ long, and 80 μ broad. These spines are not articulated with the wall, but are rigid outgrowths therefrom. Numerous strongly curved micropores pass through the wall; but are not correlated with the spines. Beneath this area, the hypodermis consists of slender columnar cells up to 30 μ long and 4–5 μ broad. When the leg is straightened, this area is more or less concealed by an overlapping thin area of the preceding segment.

Similar to this is a small area at the upper end of the first tarsal segment. In this area, the numerous spines on the surface are about 4 μ long, tapering from a broad base to an exceedingly fine apex. Here, the wall has two sharply defined layers, each about 12 μ thick. The inner layer resembles the surface, having many finely pointed dark-staining regions extending upward from the inner surface. The hypodermis beneath the surface is formed of columnar cells 15–20 μ tall (Fig. 14, C).

FIG. 15. Chorodontal organ.

- A Worker minor
- A_1 and A_2 t.s.
- B Medium worker
- B_1 l.s. upper end major worker tibia to show position of organ
- C t.s. tibia and edge of femur (f.) to show organ (m = muscles)
- C_1 and C_2 Serial sections wall of leg near end of organ
- D l.s. nerve in tibia of major

The basal region of the coxa of each leg shows a small area from which several fine hairs stiffly project. These hairs, however, are typical tactile spines, 8–12 μ long, each having a fine nerve end extending through the wall and into the fine canal occurring in each hair (Fig. 14, B).

The chordotonal organ of these two species of *Eciton* is found in the upper end of the tibia of each of the six legs (Fig. 15, B_1, C). In any one form, it varies slightly in size and in the number of its component parts: naturally, it is larger in the queen than in the workers. Invariably, it is cylindrical to slightly fusiform, passing at an angle of 30–50° from the wall on one side of the tibia to that on the opposite side. Seen from the side, it starts as a mass flattened against the wall or as a cylindrical mass of compactly grouped fibres close to the wall for a length of 40 μ to 60 μ before it turns away and crosses to the opposite wall. Throughout its length, it is clearly recognized as a compact bundle of fibres 2–3 μ in diameter, enveloped in a thin membrane which is free of filaments. In these filaments, are several ellipsoid nuclei, 4–5 μ long and 2–3 μ in diameter. These occur in two groups usually near the ends of the filament mass (Fig. 15, A, B). This mass narrows abruptly at its distal end, where it lies closely against the hypodermal layer of cells. Occasionally, this distal end is bi- or even tri-furcate. The proximal end receives a slender nerve branch originating in the lower end of the femur.

The wall at the distal end of this organ shows two different conditions. In some cases, no modifications were found: in other cases, a conspicuous small pit was found in the wall near the slender tip of the chordotonal organ (Fig. 15, C_1, C_2). This pit had a maximum diameter between 7–9 μ, and a length about one-half to two thirds the thickness of the wall where it occurred. Within this pit, several dark-staining (with haematoxylin) spirally curved structures occurred. In some cases, these were thickened areas on the surface of the wall; in others, they were free from the wall. There was no evidence of an opening from the pit to the outer surface of the wall of the tibia.

(Fig. 14, D). As in other ant species, the strigil has a pectinate spur, a bristle-fringed concavity opposing the spur and a large gland in the upper part of the tarsus.

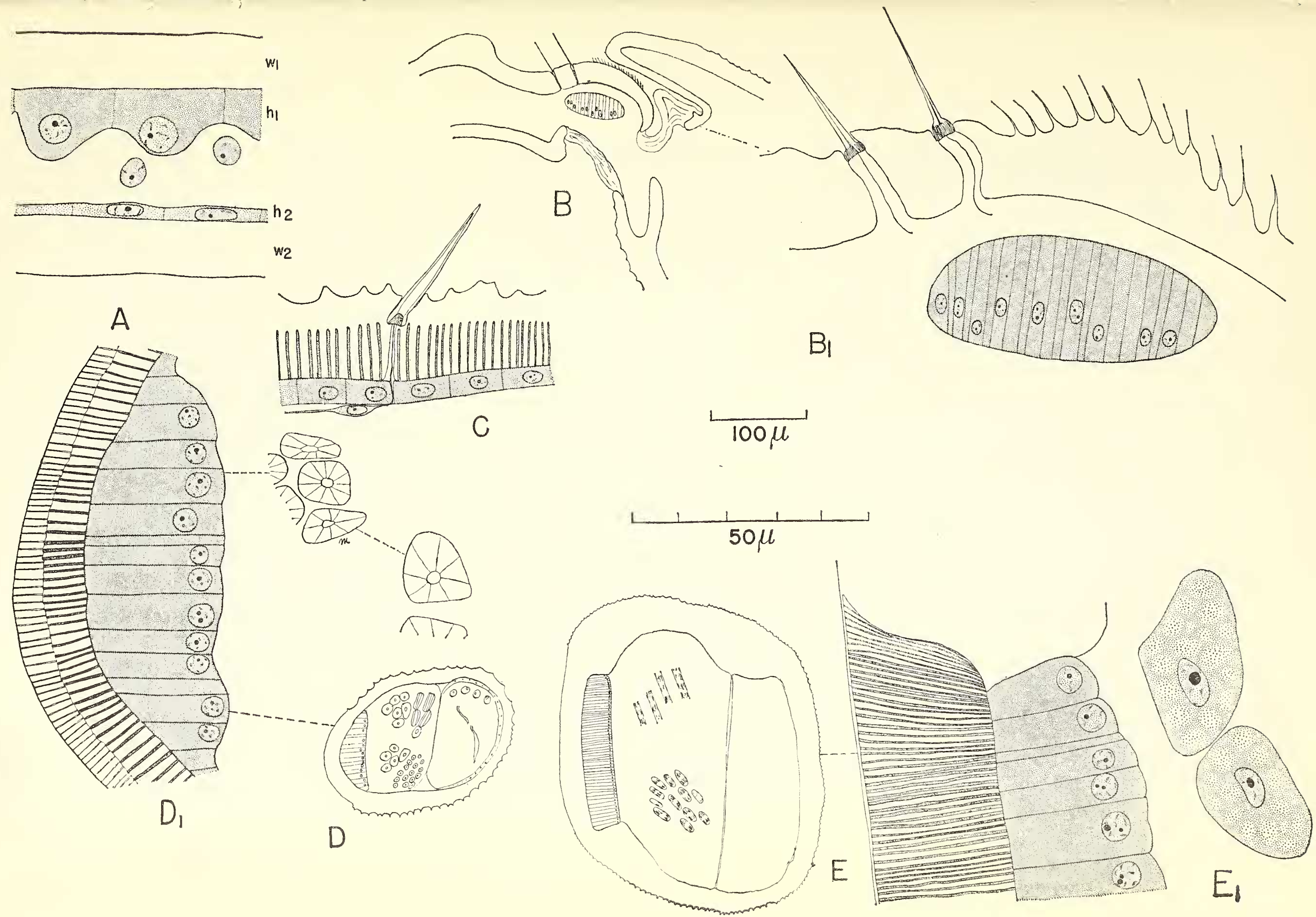
The pectinate spur is a nearly solid chitin mass, the toothed edge of which has a sigmoid outline. The base of this spur is a flattened disc around the edge of which the membrane from the lower end of the tibia to the upper end of the metatarsus is fastened.

The teeth of the concavity opposing the spur decrease uniformly from those of the upper end, 50–60 μ long, to those of the lower end 8–12 μ long varying more in individuals of differing sizes than in a group of individuals of uniform size. With the exception of the rigid basal and apical spines, spines in this row are articulated at the base and receive a fine nerve end which passes through a large pore in the wall, and into the basal end of the spine. The spines form a compact straight row: paralleling them about 3–4 μ distant, is an irregular narrow row of fine pores (Fig. 14, D_1, D_2). This irregular row may be as much as 12 μ wide in its greatest breadth, but near the end becomes a single row of coarse pores (Fig. 14, D_2). The fine pores are about 0.3 μ in diameter, the large ones about 1 μ.

These pores extend through the epicuticle; beneath that and through the remaining thickness of the wall, the latter becomes a spongy mass in which the very fine pores resemble lines rather than measurable pores (Fig. 14, D_3).

The basal end of the wall of the metatarsus is extremely irregular; one feature is a long thick incurved tooth projecting opposite the base of the pectinate spur. Along the edges of this tooth and around the rim of the wall of the segment, the membrane from the lower rim of the tibial wall is attached. When the leg is flexed, the tooth approaches the broad base of the pectinate spur which is turned away from the metatarsal surface. As the leg is straightened, the tooth moves away from the base of the spur, carrying the attached membrane with it. When the leg becomes straight or nearly so, the position of the membrane is such that the base of the spur is pulled upward into a shallow trough caused by the attachment of the membrane around the end of the tooth. The result is that the rigid pectinate spur is swung inward to press against the row of coarse spines opposing it on the tarsus.

In its simplest form, found in minor workers the metatarsal gland is an elongate kidney-shaped aggregate of cells. Penetrating to the center of this, is a mass of fine fibrous tissue. These are the fibres mentioned above as opening through the minute



w1
h1
h2
w2
A
B
B1
C
100 μ
50 μ
m
D1
D
E
E1

pores forming an irregular row alongside the row of strong spines. The cells of this gland are irregular, and continuous with the hypodermal layer (Fig. 14, E)).

In larger forms and especially in the queens, this gland is much larger, filling a large part of the body of the metatarsus for approximately half its length. In this, as in all but the minor forms, the glandular cells form an elongated mass, shaped like a flounce, the edge (when viewed from the proper angle) forming an irregularly sinuous row of varying thickness. Beneath this sinuous mass, the cell layers partly surround an elongate fibrous mass extending the entire length of the gland. This fibrous mass sends similar tissue into the central part of the cellular flounces described above. The maximum width of the cellular mass may be 65–70 μ in major workers and soldiers and 80 μ in queens (Fig. 14, E_1).

Another specialized feature in the leg is an elongate mass of columnar cells, usually forming a layer continuous with the hypodermis (Fig. 16, D, E). Occasionally the continuity of the hypodermis with the columnar layer is limited to a small part of this mass of cells, which extends upward from the base of the tibia for one-third to one-half the length of the tibia. In rare examples, these cells extend nearly the entire length of the tibia, its upper end and the chordotonal organ appearing in the same transverse section. The actual location of this structure varies. The columnar cell mass is usually parallel to the thin septum that separates the tibia into two longitudinal chambers;

FIG. 16. Hypodermis modifications.

- A t.s. labrum, dorsal wall (w_1), thick hypodermis (h_1) and ventral wall (w_2) with thin hypodermis (h_2)
- B l.s. apex of scape and base of flagellum
- B_1 Detail similar area to show fine bristles on wall surface of flagellum base and thickened lenticular region of hypodermis
- C l.s. tibia to show wall, hypodermis and nerve passing through wall into base of small tactile spine
- D t.s. upper part of small worker tibia
- D_1 Two distinct layers of wall, greatly thickened area of hypodermis (m = muscle fibers
- E t.s. tibia near upper end to show thick hypodermal structure sunk into depressed area of body wall
- E_1 Detail similar thick hypodermal region plus two oenocytes

Scale: B, D and E = 100 μ scale; others = 50 μ scale but in rare cases, one edge of the mass adjoins the attachment of one edge of the septum to the wall of the tibia. Externally, the extent of this cell mass is vaguely indicated by the sparsity or absence of hairs from the wall surface over it, and by the unusually smooth wall surface. The shape of this modified area varies as much as does its extent. Often it has a rectangular outline with the long sides nearly straight, or bulging slightly, and with a rounded triangular apical region. Less frequently, it has a triangular outline, though the lateral sides do bulge slightly and the apex is often rounded. In one other aspect does this cell mass vary strikingly. This is shown in transverse sections of the leg (Fig. 16, D, E). In some legs, this cell mass is sunk into a depression in the wall of the tibia, to such an extent that the inner surface of the wall is almost continuous with the inner surface of the columnar cells. In such individuals continuity with the hypodermal layer may be lost. In these sunken cases, the apical region of the columnar cell is only a single cell wide. Frequently, the transition from hypodermis to columnar cells is gradual with transverse sections of the columnar layer having a biconvex outline. Finally, the modified layer is abruptly formed, continuous with the thin hypodermis, but with the columnar mass of cells projecting prominently into the lumen of the tibia. The wall over this layer of cells is variously modified, sometimes showing two sharply distinct layers with non-continuous micropores in each; in others, there are larger micropores extending through the entire thickness of the cuticle, but never through the distinct thin epicuticle (Fig. 14, D, E).

The dimensions of the several parts described here vary slightly (more, of course, if one sets the dimensions of the structures of minor workers against those of the queen): the columnar cells are from 30–35 μ tall; the overlaying chitin wall 16–18 μ thick; the epicuticle 0.6–08 μ. The maximum width of the modified layer varies from 160 μ to 190 μ in workers of the same size.

INTERNAL PARASITES

One more subject though not a matter of anatomy will be considered. During the course of this study, a question frequently asked was whether I observed parasites in *Eciton*. On the basis of material studied the answer is the *Eciton* is free from parasitic organisms. In the large number of specimens examined (including larvae, pupae, and adults of all forms) only two individuals contained anything identifiable as an internal parasitic organism.

In a single large worker pupa, one of many collected May 28, 1946, the form of the mature worker was already clearly outlined, and all organs though recognizable within the wall were only vaguely indicated. The parasitic organism was found generally dispersed in the head, the thorax and the gaster. None occurred in the nerve centers, either brain or ganglia.

In some regions, it was found in small numbers, and widely separated; in other regions, the parasite was found in large

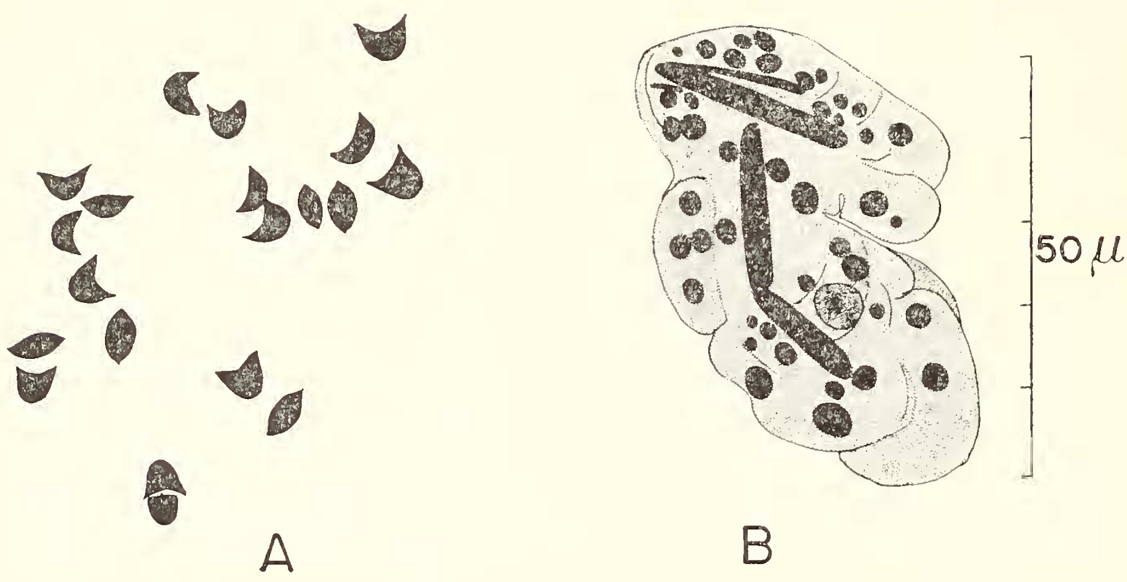


Fig. 17. Parasites found in *Eciton*.
A Small parasitic organism found in late worker pupa
B One of several small objects found in each of several of the aeration chambers of one queen only

numbers, densely aggregated. The parasite was a unicellular organism (Fig. 17, A), having the form of a coarse crescent with bluntly pointed ends. Size varied from 5 by 3 μ to 4.8 by 4 μ to a conspicuously small one measuring 3.5 by 2.5 μ. The thickness was 2.2–2.5 μ. No other specimen from this collection or any other collection, contained a single parasite.

The second object is a very different one. Looking at the small pores called "aeration pores" above, has led some to ask whether foreign organisms (that is, parasites or whatever) passed through these pores and eventually into the large chambers to which the tube led. In only one mature queen of *E. hamatum*, have I observed foreign bodies in "aeration chambers" (Fig. 17, B). They vary in size (a small one measuring 58 by 33 μ; a large one 70 by 24 μ) ; and in shape. All hold the haematoxylin stain, the black color usually concealing details. Occasional specimens show the presence of what may be a few nuclei 4–6 μ in diameter. They are found in large irregular cells, much like stomach cells in shape and association. They also contain elongate structures that may be masses of muscle fibres; and many dark round globules which could be a substance similar to the fat-globules present in adipocytes. Some are obviously formed into segments vaguely suggesting head, thorax and abdomen, the first bent down more or less closely against the second. There is no sign of appendages.

Whether these be organisms or merely some inorganic fluid condensed after passing into the bladder, must remain unanswered here. It does indicate that material can upon rare occasions pass into the body through these pores.

No other foreign object or organism was seen in any specimen in this study.

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